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Original Article

Small-scale demographic structure suggests preemptive behavior in a flocking shorebird

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Under the ideal-free distribution, omniscient individuals with similar habitat requirements that are free to move should be distributed such that no individual can improve fitness by changing sites; deviations would indicate trade-offs and constraints on ranging behavior. We studied site occupancy and annual survival in red knots *Calidris c. canutus* at their main wintering area Banc d'Arguin, Mauritania. We collected mark-resighting data at 2 high-tide roosts (A and B) that were only 3 km apart and within sight. Birds were faithful to their roosts and foraged in nearby intertidal areas, with no overlap between birds from A and B. Shellfish-rich seagrass beds were of greater abundance for birds roosting at A than at B. During 8 winters, we found different sex ratios (48% and 58% males at A and B, respectively) and different proportion of juveniles (22% and 45%) at the 2 roosts. Adult annual survival was higher at A (0.83 ± 0.01 standard error [SE]) than at B (0.81 ± 0.03). Though rare, between winter season movements were 3 times more frequent from B to A than vice versa, indicating that knots can assess the differences in site quality: birds behaved as if they were "ideal". As larger females and older birds occurred more at A, differences in competitive ability might maintain the site occupancy pattern. As females return from the high Arctic breeding grounds first, and adults return before juveniles, priority of occupancy may also play a role. Such an advantage of arriving earlier would represent a seasonal carryover effect. **Key words:** *Calidris canutus canutus*, capture–recapture models, carryover effect, high-tide roost, ideal preemptive distribution, multi-state models, seagrass, sex ratio, site fidelity, survival. [*Behav Ecol*]

INTRODUCTION

Selecting an area to live is crucial to all animals, as individuals that occupy sites with greater foraging success and lower predation risk potentially have higher reproductive success and survival, and realize higher fitness (Fretwell and Lucas 1970; Stephens and Krebs 1986; Cresswell 1994). Site selection is especially important for seasonally migrating animals that show drastic shifts in the habitats they use in the course of an annual cycle (Piersma 2012), with the caveat that what happens at one place might affect what happens at others (Harrison et al. 2010). Documenting and understanding such "carryover" mechanisms is crucial when attempting to determine in which areas, and during which time of the year, a population may experience ecological bottlenecks (Runge and Marra 2005; Buehler and Piersma 2008).

Under density-dependent habitat selection, the simplest model for site occupancy by individual animals attempting to maximize fitness is the ideal-free distribution (IFD; Fretwell and Lucas 1969; Fretwell 1972). Assumptions of the IFD are two-fold: animals are able to identify and settle in sites where fitness rewards are highest (i.e., the animals are "ideal") and

individuals are not constrained in their movements by competitive differences or travel costs (i.e., the animals are "free") (Fretwell and Lucas 1970; Fretwell 1972). For equal competitors, the IFD predicts that no individual can improve fitness by changing sites. A further development of the IFD, hereafter called the "phenotype-limited distribution", takes into account that competitive abilities may differ among phenotypes and predicts equal fitness within phenotypes (Parker and Sutherland 1986). A simple alternative to the IFD is the ideal preemptive distribution, where individuals choose to settle in the best unoccupied site available, which then becomes unavailable for other individuals (Pulliam and Danielson 1991). Empirical evidence for various distribution types is poorly known, as their investigation requires knowledge on the occurrence of quality differences between alternative habitats and the study species' settlement decisions within the annual cycle.

Shorebirds are a highly mobile group of animals and have sophisticated site-sampling processes that operate at larger spatial scales than most other animals (e.g., Piersma et al. 1993; van Gils et al. 2006; Quaintenne et al. 2011). Some species show despotic behavior such as the defence of feeding territories (Turpie 1995; Johnson et al. 2001), in others interference is absent or cryptic (Vahl et al. 2005; Bijleveld et al. 2012), and these species tend to live in flocks (Myers et al. 1979; Myers 1980). A good example of a densely flocking species is the long-distance migrating, molluscivore red knot *Calidris canutus* (van Gils and Piersma 2004). During the nonbreeding period, red knots form flocks of up to several thousand individuals foraging in extensive

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mollusc-rich intertidal habitats (Piersma et al. 1993, 2005; Folmer et al. 2010). Females are slightly larger than males (Dick et al. 1976; Tomkovich and Soloviev 1996), but the sexes are indistinguishable in the field, and red knots are regarded as a monomorphic species.

Based on distribution patterns at different spatial and temporal scales, red knots wintering at north temperate latitudes have variously been shown to behave ideal but not free, when followed across a single western European coastal wetland site over the period of a week when costs of moving were relatively high (van Gils et al. 2006), and both ideal and free, when followed across all western European coastal wetlands over a whole winter when relative costs of moving around were low in relation to distance travelled (Quaintenne et al. 2011). In both cases, the cost of moving between sites was related to energetic costs of flying rather than to differences in competitive abilities or preemptive behavior, and red knots acted as if they had perfect knowledge about the relative quality of alternative foraging areas. Red knots wintering on tropical Banc d'Arguin, Mauritania, West Africa, have much smaller home-ranges and greater site-faithfulness than birds wintering in temperate areas (Piersma et al. 1993), a difference explained by the more predictable foraging in West Africa (Leyrer et al. 2006). With their small ranging distances, we expected red knots at Banc d'Arguin to behave just as ideal and free as their conspecifics in western Europe. Yet, 8 years of red knot observations showed a consistent segregation according to sex and age on a small spatial scale both at high-tide roosts and in foraging areas, indicating deviations from the IFD. Here we compare 2 nearby sites on the basis of food-related habitat features and survival. We examine patterns of site occupancy and differences in site-specific survival prospects using mark-resighting data and multistate models and suggest that interseasonal carryover mechanisms might contribute to the observed distribution patterns.

MATERIALS AND METHODS

Study area

Our study site at Iwik Peninsula (Dakhlet Nouadhibou region, Mauritania, West Africa) is a small section of Banc d'Arguin, the main nonbreeding grounds of the Afro-Siberian red knot subspecies *C. c. canutus* (Piersma et al. 1992; Leyrer et al. 2006).

Assessing habitat quality by means of satellite images

On Banc d'Arguin, red knots preferentially feed on dense muddy seagrass (Altenburg et al. 1982), a habitat that contains higher densities of mollusc prey and offers higher intake rates than the sandy mudflats (Honkoop et al. 2008; J.A. van Gils, unpublished data). The distribution of seagrass beds in the intertidal foraging area of red knots at Banc d'Arguin were analyzed as variances in "Normalized Differences Vegetation Indices" (NDVI) (Ferguson and Korfmaier 1997; Mumby et al. 1997) obtained from 5 suitable Landsat images (18 December 2001, 22 January 2003, 9 January 2007, 11 September 2009, and 17 January 2010; freely downloadable at <http://landsat.usgs.gov>). Landsat images were considered suitable when clouds were absent and when the image was taken during low tide. NDVI values were calculated for both sites (on the basis of pixels of 30 by 30 m). Because we have used different satellites for our study (Landsat 7 and 5) and because the sensor's radiometric characteristics change over time since satellite launch, a radiometric calibration was needed (Chander, Markham and Helder 2009) to make the NDVI estimates comparable among images. For this purpose we used the image from 17 January 2010 as a reference.

Capture, marking and observation methods

During the 8-year study, capture and resighting efforts were conducted during 3-week expeditions in November/December of 2002–2009. Using mist nets, red knots were captured around new moon spring tides at 2 high-tide roosts that were <3 km apart: Abelgh Eiznaya (A, 19°54'N, 16°19'W) and Baie d'Aouatif (B, 19°54'N, 16°17'W). In this study, we include data from 1313 birds individually marked with unique combinations of colour-rings (Piersma and Spaans 2004). Of these birds, 789 different individuals were resighted after release during a total of 2822 observations. About 30–40% of the marked individuals were resighted annually in the first 2 years after capture. Ten experienced colour-ring readers scanned the total study area along the shoreline track every day (Figure 1, and see Figure 2 in Leyrer et al. 2006). Observations on mudflats away from shore started in 2004, and it increased from 50 observation sessions in 2003 to 80–120 sessions in the after years, with a maximum of 230 sessions in 2006 when weather conditions were exceptionally good for visiting the offshore mudflats. An observation session is defined as the time (1–3 h) a single observer spent in an area, and observation sessions were equally distributed over all areas.

Biometrics and demographic structure

Red knots were aged according to Prater et al. (1977), using the occurrence of white/black fringed back feathers and wing coverts to distinguish hatch-year birds (juveniles) from older birds (adults). We recorded culmen length (± 0.1 mm), wing length (± 1 mm), and tarsus length (± 0.1 mm). Body mass was measured within 4 h of capture (± 1 g). A blood sample of 5–20 μ l was collected from the brachial vein and stored in 96% ethanol for molecular sexing. Red knots captured in 2002–2006 were sexed with primers P2/P8 (Griffiths et al. 1998), which were verified for red knots by Baker et al. (1999). To avoid sexing errors due to potential length polymorphisms in the Z-intron of the CHD gene (Casey et al. 2009; Schroeder et al. 2010), primers 2602F/2669R (Fridolfsson and Ellegren [1999], modified for shorebirds by O. Haddrath, unpublished data) were used from 2007 onwards.

We used R 2.14.0 statistical software (R Development Core Team 2011) for all statistical analyses. We used binomial logistic regression to test for differences between sex ratios (females vs. males) or age ratios (juveniles vs. adult) at the 2 sites. We used linear regression models with sex, age, and site (as factors) as explanatory variables to assess potential differences in structural body size or body mass. Body mass can vary with individual variation in body size or in nutritional stores (van der Meer and Piersma 1994). Wing, tarsus and bill length measurements were analyzed in a Principal Component Analysis. PC1 explained 83% of the variation on structural body size and had positive loadings for the 3 morphometrics. The residuals of a linear regression model of body mass against PC1 as an index of size were used to compare differences in body stores between the 2 sites ($\beta \pm \text{SE}$: 1.15 ± 0.04 , $t = 30.41$, $P < 0.001$; $n = 1475$). We selected the most parsimonious model by stepwise deleting higher interaction and other nonsignificant terms.

Analyzing site fidelity and survival

Capture and resighting data were combined to create encounter histories for estimating demographic parameters with multistate models (Arnason 1973; Nichols and Kendall 1995). Multistate models offer site-specific estimates of apparent survival ϕ (phi), and the transitional probability of

movement among sites Ψ (psi), corrected for encounter rates p . Detections of red knots in the encounter histories were coded by site (A = Abelgh Eiznaya, B = Baie d'Aouatif, 0 = not seen), and the site-specific transition parameters (Ψ^{A-B} , Ψ^{B-A}) described the probability of movement for individuals switching between the 2 sites. To restrict the number of parameters to be estimated in the multistate models, which increases their precision, we made 3 *a priori* assumptions.

First, the habitat used by red knots at Banc d'Arguin is mainly open mudflats and beaches without vegetation. All birds forage on open mudflats and assemble at the same high-tide roosts, and we did not expect differences in resighting probability between sexes or age classes. Because resighting effort varied between years and sites, we modeled p as a function of site and year in all models. Second, estimates of ϕ and Ψ were modeled time independent (no effect of year), but we tested for differences and interactions between sex, age, and site. Third, analyses of a subset of the data indicated that a time-since-marking (tsm) effect explained most of the variation in annual survival (Leyrer 2011; Leyrer et al. in review). A tsm effect implies that apparent survival during the first year after capture (ϕ^1) is different from subsequent years (ϕ^{2+}), which may be caused by the presence of transients among the captured birds (individuals that pass through the study area to other nonbreeding sites) or potential handling effects (Sandercock 2006). We included a tsm effect in our global model. Because all individuals were considered adult after their second calendar year, the effect of age on survival ϕ could only be tested in models including a tsm effect.

Our global model was $\phi_{\text{sm} \times \text{age} \times \text{sex} \times \text{site}} p_{\text{site} \times \text{year}} \Psi_{\text{age} \times \text{sex}}^{A-B} \Psi_{\text{age} \times \text{sex}}^{B-A}$, and we tested goodness of fit using the median- \hat{c} test implemented in the MARK software (ver. 6.0, White and Burnham 1999). The estimated \hat{c} was 1.01 ± 0.02 SE; to control for overdispersion, \hat{c} was adjusted accordingly. Model selection was based on Akaike's information criterion corrected for small sample size and overdispersion (QAIC_c). The candidate model set consisted of 192 combinations of parameterizations for ϕ and Ψ . All models were constructed and run in program R (ver. 2.14.0) using the RMark package (ver. 2.0.8, Laake 2011) as an interface for program MARK (ver. 6.0, White and Burnham 1999). We show model-averaged estimates of survival, transition, and resighting probabilities.

RESULTS

Habitat quality and high-tide roost use

Seagrass cover was denser at Abelgh Eiznaya (high-tide roost A) than Baie d'Aouatif (roost B) in all years of study (Figure 1). As denser seagrass cover is associated with higher prey density, Abelgh Eiznaya provided better foraging conditions than Baie d'Aouatif.

In all years, we captured relatively fewer males ($48 \pm 3\%$ SE) and fewer juveniles ($22 \pm 6\%$) at A than at B (males: $58 \pm 2\%$ SE, $\beta \pm \text{SE}$: -0.41 ± 0.11 , $z = -3.58$, $P \leq 0.001$; juveniles: $45 \pm 8\%$, $\beta \pm \text{SE}$: -0.74 ± 0.12 , $z = -6.21$, $P \leq 0.001$, $n = 8$ winters, Figure 2).

Overall, red knots were larger at A and female red knots were distinctly larger than males (Table 1): males had shorter wings (A: 167 ± 5 (mm \pm standard deviation [SD]); B: 166 ± 5) than females (A: 173 ± 5 ; B: 171 ± 5), shorter culmen (A: 34.4 ± 1.7 ; B: 34.1 ± 1.6) than females (A: 36.3 ± 1.7 ; B: 35.9 ± 1.7), and shorter tarsi (A: 32.4 ± 1.2 ; B: 32.2 ± 1.3) than females (A: 33.0 ± 1.3 ; B: 33.0 ± 1.2), and males were lighter (A: 118 ± 8 [g \pm SD]; B: 116 ± 8) than females (A: 129 ± 8 ; B: 127 ± 9). Also, adults had longer wings (A: 172 ± 5 ; B: 171 ± 5) than juveniles (A: 165 ± 4 ; B: 165 ± 4), and juvenile males had the shortest wings (A: 163 ± 3 ; B: 163 ± 3).

Differences in annual survival and movement patterns

Thirteen models differed in $\Delta\text{QAIC}_c < 2$, describing variations in annual survival ϕ as a function of tsm, age, sex, and/or site and variations in movement Ψ as a function of site, age, and/or sex (Table 2; results of all candidate models tested are provided in Table S, electronic supplement). Resighting probability p differed between the sites and among years (Table 3). Apparent survival ϕ differed between the 2 sites, with both age classes having higher annual survival at A than at B. Apparent annual survival of adults was 0.83 ± 0.01 (estimate \pm SE) at A and 0.81 ± 0.03 at B, juvenile annual survival was 0.78 ± 0.04 at A and 0.75 ± 0.04 at B. At both sites adult survival was lower in the first year after marking than in subsequent years (tsm effect) (Table 3). With 20% or less, the overall probability of moving to the other site between winter seasons was low (Table 3). Yet, directional movements of both adults and juveniles were 3 times more frequent from the lower survival site B to the higher survival site A than in the opposite direction (Table 3).

DISCUSSION

We documented differences in foraging conditions and demographic structuring at 2 adjacent sites. High-tide roost A (Abelgh Eiznaya) predominantly hosted the larger sex (females) and the older (more experienced) age class (adults). In addition, birds of similar sex were generally larger at A than at B (Baie d'Aouatif). Given the greater proportion of seagrass, birds at site A would also encounter higher intake rates, which may have allowed for a slightly higher annual survival. Confirming a previous study showing high site-faithfulness within a winter season (Leyrer et al. 2006), there was little interchange between the two nearby sites across all years. As red knots are notorious flyers (*canutus* knots routinely migrate ~20 000 km each year; Piersma et al. 1992; Shamoun-Baranes et al. 2010), a lack of movement between the 2 sites suggests that individual red knots were somehow restrained from moving freely. Individuals that did move switched from the lower survival site B to the higher survival site A. Under the ideal-free distribution, we expected a random distribution of the 2 age and sex classes, and no survival differences between sites, so clearly we have to reject this hypothesis (Table 4). That most movements between years occurred toward the best site suggests that the birds were well aware of the site quality differences (i.e. they were ideal but unable to freely move between sites).

The phenotype-limited distribution takes into account that phenotypes differ in their competitive ability (Parker and Sutherland 1986). Unlike the related western sandpiper *Calidris mauri*, in which sex and age related culmen length affects both microhabitat segregation and nonbreeding distribution (Mathot et al. 2007), in red knots foraging habitat choice has previously been explained by phenotypic variations in gizzard size rather than by sex- or age-related traits (van Gils et al. 2005). Red knots eat hard-shelled molluscs that need to be crushed and processed internally, and gizzard size constrains the rate of food intake. Gizzard mass is a highly plastic trait (Dekinga et al. 2001), but the growth and maintenance of a large gizzard takes time and energy (van Gils et al. 2007). Indeed, gizzards of red knots measured in April 2007–2009 using ultrasonography (Dietz et al. 1999) were somewhat smaller at A ($8.8 \text{ g} \pm 2.9$; $n = 9$) than at B ($10.5 \text{ g} \pm 3.4$; $n = 77$), but the differences were not significant (*t*-test: $t = 1.6$, $\text{df} = 10.9$, $P = 0.14$). Besides offering more and possibly higher quality food, A also might be the safer site. Observations on vigilance patterns in foraging red

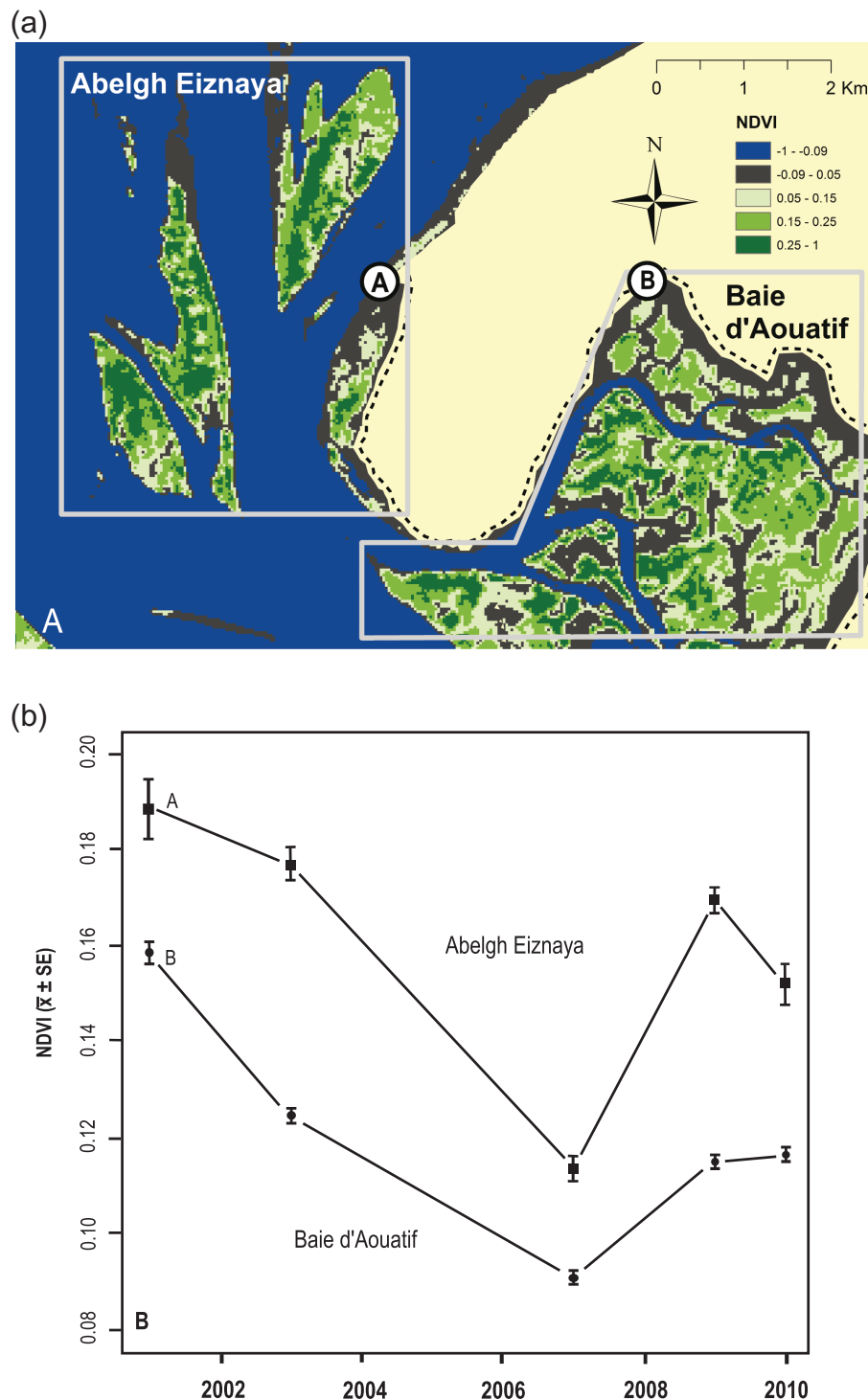


Figure 1

(a) The distribution of seagrass beds in the intertidal foraging area of red knots at Banc d'Arguin, Mauritania, shown as variances in NDVI, extracted from a Landsat 7 image taken at 22 January 2003. Yellow areas show mainland, blue areas show water, grey areas show bare intertidal mudflats, and green colors indicate various NDVI intensities (see legend). Grey-bordered blocks indicate intertidal foraging areas connected to the respective high-tide roosts A and B (white circles). The dashed line shows the shoreline walked daily to scan for marked birds. (b) NDVI values (mean \pm SE) plotted over time for both foraging areas. NDVI values for the foraging areas were higher for A (Abelgh Eiznaya) than for B (Baie d'Aouatif) (Student's $t = 6.2$, $df = 4$, $P < 0.05$), suggesting that A offered higher food densities than B.

knots indeed indicate lower vigilance and thus lower predation danger at A than at B (van Gils et al., unpublished data). We also detected differences in survival between adult and juvenile red knots. This is consistent with the observation that juveniles suffer higher annual mortality than adults

due to predation by large falcons (van den Hout et al. 2008). This and the observed small-scale segregation of the age classes suggest that the phenotype-limited distribution explains the age-dependent habitat choice in Mauritanian red knots (Table 4).

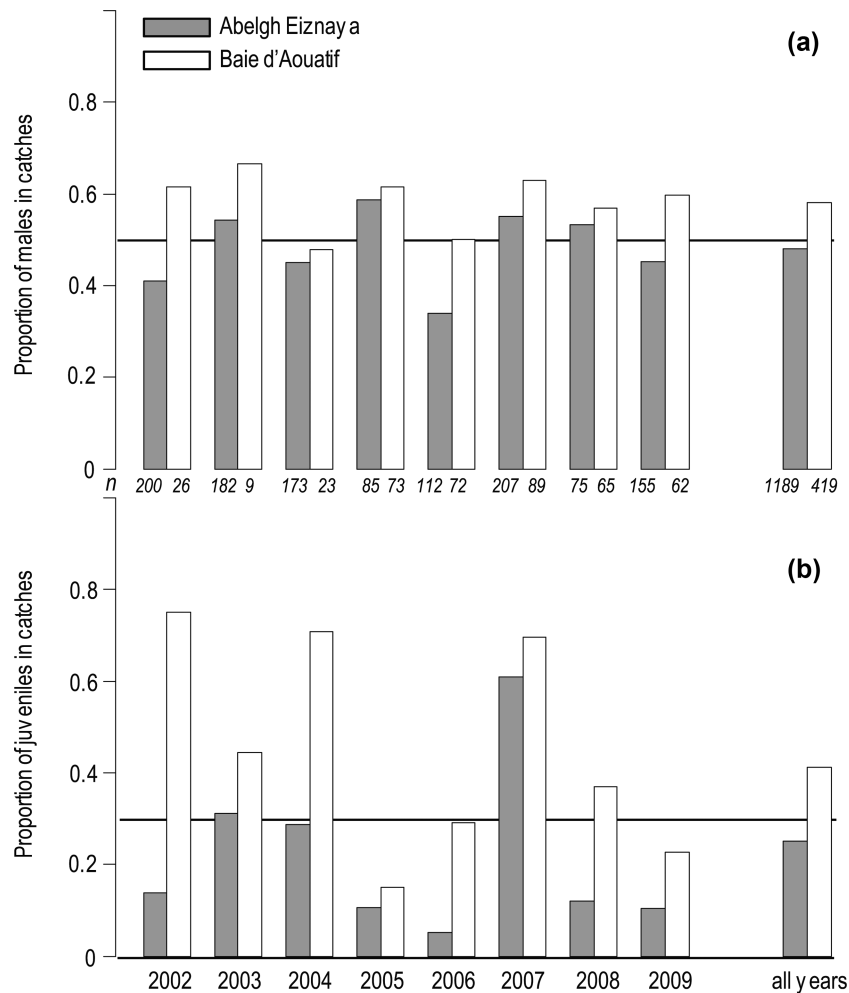


Figure 2
Proportions of (a) males and (b) juveniles among captures at Abelgh Eiznaya and Baie d'Aouatif, November–December 2002–2009. Numbers in italics indicate the numbers of red knots examined. Lines at 0.5 (a) and 0.3 (b) indicate equal sex ratios and average juvenile/adult ratio across all years, respectively.

Table 1
Summary of linear regression models of wing, culmen, tarsus and body mass on sex, age, and/or capture location (site) Abelgh Eiznaya or Baie d'Aouatif in wintering red knots

		Estimate	SE	t value	P value
Wing ^a	Intercept	167.18	0.27	625.88	<0.001
	Age	7	0.21	22.29	<0.001
	Sex	−3.97	0.36	−11.1	<0.001
	Sex:age	−0.95	0.43	−2.2	0.028
Culmen ^b	Intercept	35.95	0.1	360.96	<0.001
	Sex	−1.84	0.09	−21.19	<0.001
	Site	0.31	0.10	3.13	0.002
Tarsus ^c	Intercept	32.86	0.07	440.07	<0.001
	Sex	−0.63	0.06	−9.77	<0.001
	Site	0.15	0.08	2.02	0.04
Body mass ^d	Intercept	0.09	0.41	0.21	0.8
	Age	3.23	0.42	7.7	<0.001
	Sex	−4.64	0.39	−11.9	<0.001

Nonsignificant (interaction) terms were dropped and models rerun. Regressions on body mass were tested on size corrected body mass. The parameter estimates for sex are given for males in relation to females, for age: adults in relation to juveniles, for site: Abelgh Eiznaya in relation to Baie d'Aouatif.

^a $F_{3, 1471} = 525.2$, $r^2 = 0.52$, $P < 0.001$.

^b $F_{2, 1472} = 236.9$, $r^2 = 0.24$, $P < 0.001$.

^c $F_{2, 1472} = 51.9$, $r^2 = 0.06$, $P < 0.001$.

^d $F_{2, 1472} = 109.7$, $r^2 = 0.13$, $P < 0.001$.

Table 2

The most parsimonious multistate models ($\Delta\text{QAIC}_c < 2$) with estimates of apparent annual survival ϕ and movement probability Ψ depending on time-since-marking (tsm), age class (age: adult/juvenile), sex (male/female) and site (Abelgh Eiznaya (A)/Baie d'Aouatif (B)) for red knots at Iwik Peninsula, Banc d'Arguin, Mauritania, West Africa, in winters 2002–2009. In all models, resighting probability was modeled as a function of site and year.

Model	NP	QDeviance	ΔQAIC_c	QAIC_c weight
$\phi_{\text{tsm+site}} \hat{p}_{\text{site+time}} \Psi_{\text{age}}^{A-B} \Psi_{\text{const.}}^{B-A}$	14	1584.86	0	0.039
$\phi_{\text{tsm+site}} \hat{p}_{\text{site+time}} \Psi_{\text{age}}^{A-B} \Psi_{\text{const.}}^{B-A}$	13	1587.30	0.41	0.031
$\phi_{\text{tsm}} \hat{p}_{\text{site+time}} \Psi_{\text{age}}^{A-B} \Psi_{\text{const.}}^{B-A}$	13	1587.53	0.65	0.028
$\phi_{\text{tsm*age+site}} \hat{p}_{\text{site+time}} \Psi_{\text{age}}^{A-B} \Psi_{\text{const.}}^{B-A}$	15	1583.70	0.86	0.025
$\phi_{\text{tsm*age}} \hat{p}_{\text{site+time}} \Psi_{\text{age}}^{A-B} \Psi_{\text{const.}}^{B-A}$	14	1586.02	1.16	0.022
$\phi_{\text{tsm*age+site}} \hat{p}_{\text{site+time}} \Psi_{\text{const.}}^{A-B} \Psi_{\text{const.}}^{B-A}$	14	1586.05	1.19	0.021
$\phi_{\text{tsm+site}} \hat{p}_{\text{site+time}} \Psi_{\text{age}}^{A-B} \Psi_{\text{age}}^{B-A}$	15	1584.08	1.24	0.021
$\phi_{\text{tsm}} \hat{p}_{\text{site+time}} \Psi_{\text{const.}}^{A-B} \Psi_{\text{const.}}^{B-A}$	12	1590.22	1.32	0.020
$\phi_{\text{tsm+site}} \hat{p}_{\text{site+time}} \Psi_{\text{const.}}^{A-B} \Psi_{\text{age}}^{B-A}$	14	1586.51	1.65	0.017
$\phi_{\text{site}} \hat{p}_{\text{site+time}} \Psi_{\text{age}}^{A-B} \Psi_{\text{const.}}^{B-A}$	13	1588.55	1.67	0.017
$\phi_{\text{tsm*age}} \hat{p}_{\text{site+time}} \Psi_{\text{const.}}^{A-B} \Psi_{\text{const.}}^{B-A}$	13	1588.59	1.71	0.016
$\phi_{\text{tsm+site}} \hat{p}_{\text{site+time}} \Psi_{\text{age+sex}}^{A-B} \Psi_{\text{const.}}^{B-A}$	15	1584.59	1.76	0.016
$\phi_{\text{tsm+site}} \hat{p}_{\text{site+time}} \Psi_{\text{age}}^{A-B} \Psi_{\text{sex}}^{B-A}$	15	1584.77	1.94	0.015
$\phi_{\text{tsm+sex+site}} \hat{p}_{\text{site+time}} \Psi_{\text{age}}^{A-B} \Psi_{\text{const.}}^{B-A}$	15	1584.86	2.02	0.014

$\text{QAIC}_c = 6698.50$

Table 3

Model-averaged estimates of annual apparent survival (ϕ), movement (Ψ) and resighting probability (\hat{p}), standard errors (SE), and 95% confidence intervals for eight years of observing red knots at their tropical wintering area Banc d'Arguin, Mauritania, West Africa, 2002–2009. Estimate \pm SE (95% CI)

		Abelgh Eiznaya	Baie d'Aouatif
Annual apparent survival ϕ			
Adult	ϕ^1	0.80 ± 0.02 (0.74–0.84)	0.77 ± 0.04 (0.69–0.83)
	ϕ^{2+}	0.83 ± 0.01 (0.80–0.86)	0.81 ± 0.03 (0.75–0.86)
Juvenile		0.78 ± 0.04 (0.70–0.84)	0.75 ± 0.04 (0.66–0.83)
Movement Ψ			
Female	$\Psi^{A \rightarrow B}$	0.07 ± 0.01 (0.05–0.08)	$\Psi^{B \rightarrow A}$ 0.19 ± 0.03 (0.14–0.24)
Male		0.06 ± 0.01 (0.05–0.08)	0.18 ± 0.02 (0.14–0.23)
		$\Psi^{A \rightarrow A}$ 0.93/0.94	$\Psi^{B \rightarrow B}$ 0.81/0.82
Juvenile		0.09 ± 0.03 (0.04–0.18)	0.20 ± 0.04 (0.13–0.30)
		$\Psi^{A \rightarrow A}$ 0.91	$\Psi^{B \rightarrow B}$ 0.80
Resighting probability \hat{p}			
2003		0.30 ± 0.04 (0.23–0.38)	0.25 ± 0.05 (0.17–0.35)
2004		0.37 ± 0.03 (0.32–0.44)	0.32 ± 0.04 (0.24–0.41)
2005		0.45 ± 0.03 (0.40–0.50)	0.39 ± 0.05 (0.31–0.48)
2006		0.55 ± 0.03 (0.49–0.60)	0.49 ± 0.04 (0.41–0.57)
2007		0.61 ± 0.03 (0.55–0.66)	0.55 ± 0.04 (0.47–0.63)
2008		0.51 ± 0.03 (0.46–0.57)	0.45 ± 0.04 (0.38–0.53)
2009		0.58 ± 0.03 (0.51–0.64)	0.52 ± 0.04 (0.44–0.60)

Table 4

Summary of the main predictions of three distribution models and our results

Prediction fitness differs between	Model			Our data
	Ideal-free distribution	Phenotypic distribution	Preemptive distribution	
Phenotypes	NO	YES	NO	NO (sex) YES (age)
Sites	NO	YES	YES	YES
	Fretwell and Lucas 1969	Parker and Sutherland 1986	Pulliam and Danielson 1991	

Also the sex classes were small-scale segregated. However, in spite of the differences between sites A and B in adult survival, we found no survival differences between the sexes. This finding aligns best with the predictions of the ideal preemptive distribution model (Table 4, Pulliam and Danielson 1991). The core idea of the ideal preemptive distribution is the importance of the order of arrival: individuals that arrive first settle in the best unoccupied sites available, which then become unavailable for other individuals. In red knots, during successful reproduction, males attend their offspring for almost 3 weeks after the females have left the high Arctic breeding grounds immediately after hatch. The juveniles migrate south even later than the adult males (Tomkovich and Soloviev 1996). As a consequence, earlier arriving females can settle at the better sites, in our case site A (note though that sex- and age-related differences in arrival timing cannot explain the larger body sizes at A). In years of breeding failure, males migrate at the same time as females (Meissner 2005). Their earlier arrival might enable some males to upgrade to better sites, thus partially “compensating” for reproductive failure by subsequent survival benefits. Such an early arrival advantage would then represent an important cross-seasonal carryover effect (Harrison et al. 2010).

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